

A TAXONOMIC REASSESSMENT OF *CLARKIA CALIENTENSIS* AND
CLARKIA TEMBLORIENSIS

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ABSTRACT

The taxonomic relationships of *Clarkia calientensis* were re-evaluated in light of information accumulated subsequent to its designation as *C. tembloriensis* subsp. *calientensis*. Closeness of relationship between *C. calientensis* and *C. tembloriensis* was based on ease of crossing and on cytological pairing configurations in intertaxon hybrids. These interpretations require the assumptions that closely related species are easy to cross, and that maximum cytological configurations are known. However, extensive crossing data show that sympatric, closely related species of *Clarkia* are very difficult to cross but allopatric species cross rather readily. Furthermore, the cytological data are incomplete as maximum configurations are seldom observed, and some hybrids have not been produced. In both cases, the required assumptions are not tenable. Sterile hybrids between these two easily crossed taxa are strong evidence that they are not conspecific. Consequently, *C. calientensis* should be recognized as an independent species. Examination of floral variation in *C. tembloriensis* led to the recognition of large-flowered, protandrous forms as a new subspecies: *C. tembloriensis* subsp. *longistyla*.

Key Words: *Clarkia calientensis*, *C. tembloriensis*, crossability, hybrid sterility, outcrossing rate, translocations.

This paper is dedicated in honor of Professor F. Harlan Lewis, who passed away in December, 2008.

Clarkia calientensis Vasek (Onagraceae) occurs only in the Caliente Hills, east of Bakersfield (Vasek 1977). *Clarkia tembloriensis* occurs in the arid, Inner Coast Ranges from Alameda and San Joaquin Counties (Corral Hollow) southward to San Luis Obispo and Kern Counties (Temblor Range), and in the Caliente Hills and Tejon Hills, east of Bakersfield (Vasek 1977). They are related to each other, and to *C. exilis* and *C. springvillensis* of the Sierra foothills in Kern and Tulare Counties, as well as to the widespread *C. unguiculata* from which all four were probably derived (Vasek 1958, 1964a, 1968, 1977). The derivatives are allopatric with each other, but sympatric, or marginally so, with *C. unguiculata* at the low elevation margin of its range. These derivative species are similar to one another but were first recognized in the field on morphological traits and subsequently subjected to extensive studies of distribution, ecology, flowering, development, cytology, and breeding systems (Vasek 1977, and included references). Nevertheless, they may be difficult to distinguish as herbarium specimens.

A study was undertaken by Holsinger (1985) to determine how these species correspond with phenetic groupings. Upon completion of this phenetic study, a reinterpretation of then existing

cytogenetics, crossing relationships, and ecological data resulted in the conclusion that *C. tembloriensis* and *C. calientensis* had origins independent of *C. unguiculata*, and should be considered conspecific. Furthermore, *C. calientensis* Vasek was transferred to *C. tembloriensis* as a subspecies, *C. tembloriensis* subsp. *calientensis* Holsinger. Since then, new collections, and extensive research, particularly in population dynamics and breeding system functions have added new information and insights. The present paper reviews the available information, both old and new, and clarifies the relationships of these species.

TAXONOMIC STATUS OF *C. CALIENTENSIS*

The phenetic study by Holsinger (1985) includes two main parts: a phenetic study proper, and a reinterpretation of existing information. The phenetic study is carefully detailed and well done. A first ordination, based on petal size, ovary pubescence and stigma exertion against ovary size (length and width), determined three clusters corresponding to: *Clarkia unguiculata*, *C. exilis*, and a mixed group of *C. springvillensis*, *C. tembloriensis*, and *C. calientensis*. A second ordination of the latter group separated out *C. springvillensis* by ovary size and its purple sepals. The continued grouping of *C. tembloriensis* and *C. calientensis* could not be resolved. However, a secondary ordination of just the mixed subgroup (Fig. 3 in Holsinger 1985) showed essentially separate groupings for, not only *C. springvillensis*, but also for *C. calientensis*, and for large-flowered and small-flowered forms of *C. tembloriensis*. The

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discussion indicates that petals of *C. calientensis* are larger than those of small-flowered *C. tembloriensis* and about the same as large-flowered *C. tembloriensis*. Further, *C. calientensis* differs from both forms of *C. tembloriensis* by a more slender ovary and slightly broader leaves. Despite methodological limitations imposed by reliance on character traits of flowering herbarium specimens, the phenetic study generally agrees with a larger phenotypic study (Vasek 1977) of the same species, which enjoyed the luxury of developmental traits and larger population samples and provided an estimate of phenotypic plasticity. Both studies show a close similarity, but not identity, of *C. calientensis* with small-flowered *C. tembloriensis*.

The second part of the phenetic study is more speculative. On the basis that hybrids were readily produced between *C. calientensis* from the Caliente Hills and *C. tembloriensis* from the Temblor Range, it concludes that these two species are conspecific and did not have independent origins in *C. unguiculata* (as suggested by Vasek 1964a, 1968, 1977). This interpretation requires the assumption that closely related species are easily crossed. Closely related derivative species generally occur adjacent to parental species (Lewis and Raven 1958) and probably originated about where they are found now. With sympatric or even marginally sympatric species, some barrier to crossing must be in place upon, or soon after, origin of a derivative species. Otherwise, the original species and its derivative would cross breed back to panmixia. One possible isolating mechanism might be based on control or selection of the pollen genotypes that actually function in particular stigmas and styles. A significant body of data has been accumulating recently on this and related topics (Bowman 1987; Jones 1994; Kerwin and Smith-Huerta 2000; Smith-Huerta 1996b, 1997; Smith-Huerta and Vasek 1984). Another possible isolating mechanism is hybrid sterility occasioned, perhaps, by chromosomal translocations (Vasek 1958, 1964a, 1968). Sympatric, or marginally sympatric species of *Clarkia* are actually very difficult to cross, and some hybrid combinations have not been produced despite numerous attempts. Thus, strong isolating mechanisms are in place. In addition, the few hybrids produced are usually highly sterile, often as a consequence of chromosome rearrangements. In contrast, allopatric species are rather easily crossed (Vasek 1958, 1964a, 1968), but their hybrids are also usually sterile. In any event, the required assumption regarding crossability and the closeness of relationship is not supported.

The second part of the phenetic study also calls upon cytological data to indicate that *C. calientensis* and *C. tembloriensis* are more closely related to each other than to any other taxon of

this group. Most interspecific hybrids in this group of *Clarkia* are heterozygous for a number of translocations, often 5 or 6 (Vasek 1964a, 1968). Four or more translocations are indicated (citing Vasek 1964a) as the difference between *C. calientensis* and *C. unguiculata*, compared with only three translocation differences between *C. calientensis* and *C. tembloriensis* (citing Vasek 1968 as 1967). An interpretation like this requires that maximum translocation configurations are known for the interspecific hybrid combinations being considered. However, the former hybrid discussed here has not been produced despite 30 attempts (Vasek 1968). In the latter hybrid, the maximum configuration may or may not have been observed, since only one cell, out of 55 analyzed, showed a closed ring of 8 chromosomes. Maximum translocation configurations are seldom observed, and hence are often problematical. An attempt to construct detailed relationships based on the perception that one hybrid may have one more translocation than another exceeds the capability of the data available. The evidence, therefore, does not support the conclusion.

The second part of the phenetic study also suggests derivation of *C. calientensis* in the Caliente Hills from *C. tembloriensis* in the Temblor Range. Given the distance and the unsuitable terrain between, such an event is geographically highly improbable. *Clarkia tembloriensis* (large flower type) does occur in the upper, eastern portion, and *C. calientensis* occurs in the lower western portion, of the Caliente Hills, but they are not sympatric. *C. unguiculata* occurs between and is marginally sympatric with both. Hence, the geography would favor either *C. unguiculata* or large-flowered *C. tembloriensis* as a possible species of origin. Whereas *C. unguiculata* is well known for chromosomal innovation, *C. tembloriensis* is cytologically uniform as far as is known. Therefore, *C. unguiculata* seems a more likely source of origin for *C. calientensis*, as it likely was for *C. exilis*, *C. springvillensis*, and *C. tembloriensis*.

Finally, the sterility of hybrids between *C. calientensis* from the Caliente Hills and *C. tembloriensis* from the Temblor Range is strong evidence that the two are not conspecific. Accordingly, the evidence presented does not support the reinterpretation of data in the second part of the phenetic study. Therefore, it is recommended, that *Clarkia calientensis* be recognized at the species level.

TAXONOMY OF *CLARKIA TEMBLORIENSIS*

Floral Variation

Clarkia tembloriensis was described (Vasek 1964b) primarily from material under study from

TABLE 1. SYNOPTIC COMPARISON OF FLOWER-TYPES IN *CLARKIA TEMBLORIENSIS*. Entries for style and petal length are rounded progeny means for experimental plants grown in a greenhouse. CP = crinkled petal. ND = not determined. ¹ Estimate from a very small population in Cedar Canyon (Temblor Range) having a very high percentage of CP. ² In table 3 (Vasek and Weng 1988), samples T1 and T2 are large-flowered out crossers, and samples T3–T5 are small-flowered outcrossers.

Flower type	Large outcrosser	Small outcrosser	Small selfer	Small CP
Flower size index	78–70	66–55	54–42	42–33
Outcrossing rate (%)	87–67	58–51	26–03	61 ¹ –08
P/O ratio ²	160–148	164–141	73–30	ND
Style length – mm (mean)	22–22	19–16	13–10	13–09
Petal length – mm (mean)	24–21	19–14	15–10	11–09

Kern and San Luis Obispo counties (Vasek 1964a). Plants farther north were scarcely known and not yet available for study, but a few plants from as far north as San Benito County contributed to the species description (Vasek 1964b). Later collections and field studies established the occurrence of large-flowered populations in San Benito and Kern counties (Vasek and Sauer 1971; Vasek and Harding 1976) and introduced the concept of small-flowered and large-flowered syndromes in *Clarkia* (Moore and Lewis 1965; Vasek 1971, 1977; Holsinger 1985; Vasek and Weng 1988; Holtsford and Ellstrand 1989, 1992).

A large flower syndrome collectively includes large hypanthia, sepals and petals and long styles in an out crossing breeding system. Development of the stigma is delayed for a number of days as the style and other flower parts continue to grow. Hence the flowers attain larger size, before the stigma expands and becomes receptive (Smith-Huerta and Vasek 1984, 1987). Often, a half dozen flowers or so may open before the stigma of the first flower expands in readiness for pollination. Separation of the stigma from the anthers, both in time and space, imposes a requirement for a pollen vector (Vasek 1968).

A small flower syndrome collectively includes smaller hypanthia, sepals and petals and a shorter style associated in a breeding system capable of effecting unaided self-pollination. The stigma matures and expands, and is receptive for pollination the first or sometimes the second day of anthesis. Growth of the style stops upon stigma maturation, and growth of petals stops soon after (Vasek 1958).

The large-flowered group within *C. tembloriensis* includes only one prominent flower-type: large-flowered out crossers (Fig. 1). However, the small-flowered group includes three prominent flower-types: small-flowered out crossers, small-flowered selfers, and crinkled petals (Fig. 2).

Together, the four flower-types differ in two major variable traits and their included components: flower size and out crossing rate. A flower size index was developed for small-flowered plants by summing measurements (in mm) of petal width and the lengths of ovary, hypanthi-

um, sepal, style and petal (Vasek 1964a), and extended to large-flowered plants by adaptation of data in a study of phenotypic variation (Vasek 1977). Herbarium specimens examined for this paper fall into the same flower-size index classes, with the same ranges, as just described for experimental material.

Outcrossing rates were taken directly from the estimates of Vasek and Harding (1976) based on phenotypic traits, and of Holtsford and Ellstrand (1989) based on isozyme polymorphisms. In addition, a general indication of breeding system characteristics is afforded by the pollen/ovule (P/O) ratio, and this information is taken directly from a study by Vasek and Weng (1988). A synoptic comparison of the four flower-types is summarized in Table 1.

The type locality for *Clarkia tembloriensis* is Carneros Rocks (Vasek 1964b) on the east side of the Temblor Range (Kern County) at an elevation of about 1400 ft. This standard small-flowered self-pollinator (Fig. 2a) is common in the Temblor Range region of western Kern and eastern San Luis Obispo counties and northward to Fresno County (Cantua Creek), Merced County (Los Banos Creek), and to Alameda and San Joaquin counties (Corral Hollow). Standard small-flowered plants are fully capable of self-pollination, but some cross-pollination commonly occurs (Table 1).

Two prominent variations occur. One variant form, termed small-flowered outcrossers (Smith-Huerta, personal communication), has styles somewhat longer than those in standard small-flowered selfers, and some degree of protandry may occur (Fig. 2c). The flowers are generally a little larger, and the outcrossing rate somewhat higher, than in standard small-flowered plants (Table 1). Several small-flowered outcrossing populations occur at elevations above 2300 ft in the Temblor Range, and at lower elevations in the Red Hills (Hughes Canyon), and in the Kettleman Hills and Corral Hollow.

A second variant is termed crinkled petal (CP) in which petals are reduced to very narrow (1–3 mm wide) sepal-like, unexpanded structures in which the blade is scarcely wider than the very short claw (Fig. 2b). CP is conditioned by a single



FIG. 1. *Clarkia tembloriensis* subsp. *longistyla*. a) Five consecutive flowers (top to bottom) from flower opening through style and stigma development to pollination; b) a young flower with elongating style and immature stigma; c), an older flower with expanded stigma recently pollinated. Photographs courtesy of N.L. Smith-Huerta. The white line represents a length of 1 cm.

recessive gene and occurs in both standard small-flowered populations and in small-flowered outcrossing populations (Vasek 1964a, 1966; Smith-Huerta 1992, 1996a), and therefore has little taxonomic significance. Nevertheless, some populations may have rather high CP frequencies and CP is apparently fixed in one population near Cholame. CP plants have not been observed north of San Luis Obispo County.

The final major flower-type consists of large-flowered plants (Fig. 1a) with long styles (Fig. 1b, c), large flower parts, marked protandry and high outcrossing rates (Table 1). Large populations occur in the Griswold Hills (San Benito Co.) and Tumey Hills (Fresno Co.) and the Caliente Hills (Kern Co.). Protandrous, large-flowered plants have also been collected in Stanislaus Co. (Arroyo del Puerto: Sharsmith in 1935) and in Kern Co. (near Long Tom Mine: Smith in 1941; and near Bakersfield: Davy in 1896).

Small-flowered plants had been intercrossed experimentally in numerous combinations, with no sign of any reduction in fertility or chromosomal uniformity (Vasek 1964a). Large-flowered types had not yet been available for inclusion in the hybridization program, and subsequently were assumed to be completely interfertile with the small flowered types. This assumption has been ably documented by the elegant experimental investigations of pollen germination and pollen tube growth in both types and their hybrids (Kerwin and Smith-Huerta 2000; Smith-Huerta 1996b).

DISCUSSION AND CONCLUSION

Variation in flower size in small-flowered selfers and small-flowered outcrossers is essentially continuous (Table 1). Some populations may include both small-flowered types, at least at different times. Both types occur along the length

of the species range and are commonly adjacent in and around the Temblor Range. Interestingly, the small flowered outcrossers have high P/O ratios, comparable to those of large-flowered outcrossers, and higher than those of small-flowered selfers (Table 1).

The somewhat similar occurrence of slightly longer styles and some degree of protandry was reported in *C. exilis* (Vasek 1958), an otherwise small-flowered selfer. It is tempting to think of small-flowered outcrossers as an intermediate step in the evolution of a self-pollinating system (see Moore and Lewis 1965).

The difference between large-flowered outcrossers and small-flowered outcrossers is essentially discontinuous, especially for flower size (Table 1; and fig. 3 in Holsinger 1985). The two types have not been observed in mixed populations and their ranges apparently do not overlap. Occasionally, however, an odd plant with small flowers has been collected in a population area of a larger flower type. Two examples are known in which a small-flowered plant with short styles was collected in a locality where large-flowered plants with long styles were collected in other years: Griswold Hills: *Hesse* 2451 in 1958 and *Raven* 10866 in 1957; and Tumey Hills: *Vasek* 620505-3 in 1962 and *Sanders* 35150 in 2008. Similarly, a stunted plant with very small flowers was collected by *Smith-Huerta s.n.* in 2004 in an often-visited study population of small-flowered outcrossers in the Temblor Range. These examples of presumed phenotypic plasticity may reflect adverse weather conditions, as is commonly observed for late season or poor season reduction in size of parts (Vasek 1977; Holtsford and Ellstrand 1992). Problems of this sort are few and only minimally inconvenient.

On the basis of the evidence reviewed here, the protandrous plants with large flowers and long, exerted styles (Fig. 1a, b, c) are hereby proposed for recognition as a new subspecies, *C. temblor-*

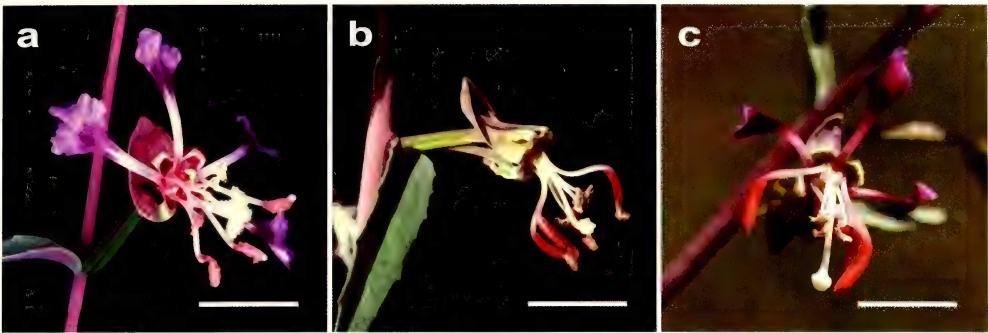


FIG. 2. *Clarkia tembloriensis* subsp. *tembloriensis*. a) A standard small flower from Cantua Creek, with a short style and a receptive stigma among anthers of about the same length; b) a flower with crinkled petals (CP) from Red Rocks near Cholame, with style and stamens about the same length; c) a small flowered outcrosser from McKittrick Road, with an elongating style and an immature stigma exceeding the anthers. Photographs courtesy of N.L. Smith-Huerta. The white line represents a length of 1 cm.

ensis subsp. *longistyla*, and the small-flowered types are proposed to constitute the residual subspecies, *C. tembloriensis* subsp. *tembloriensis*.

TAXONOMY

Clarkia tembloriensis* subsp. *longistyla Vasek subsp. nov. (Fig. 1)—TYPE: USA CALIFORNIA, San Benito County, Griswold Hills, 4.6 mi south of Panoche Road. May 4, 2008. *Sanders 35167* (holotype UCR; isotypes: CAS, DAV, MO, NY, RSA, SBBG, SD, UC, US). *Sanders 35187* (paratypes: DAV, UCR); *Sanders 35150* (paratypes: CAS, DAV, RSA, UC, UCR).

Flores hypanthiis 2–4 mm; sepalis viridibus, interdum ruberis suffusis, 14–18 mm, connatis (in 4 s), puberulentis, sine longis patentibus pilis; petalis lavandulis-roseis, interdum unumquidque cum purpurascenti macula, 17–25 mm, unguibus gracilibus integeris longitudibus 1- vel 2-plo laminis, laminis plus minusve rhombicis; stamenibus 8, extimis antheris ruberis vel lavandulis et intimis dilutioribus; stylis 17–25 mm, longiexsertis, extensis ultra stamenibus, stigmatibus non fungentibus antea 3–6 diebus postanthesin; capsulis 1.5–3 cm.

Stems erect, to 8 dm, glabrous, glaucous. **Leaves** lanceolate 2–7 cm, 0.5–2.5 cm wide, glaucous, gray-green; petioles 0–13 mm. **Inflorescence** axis in bud straight; buds reflexed. **Flowers** with hypanthia 2–4 mm; sepals 14–18 mm long, green, sometimes tinged with red, connate, puberulent, without long spreading hairs; petals 17–25 mm long, lavender-pink, often with purplish spot, with claws slender, entire, lengths 1–2 times blades, with blades more or less rhombic; stamens 8, with outer anthers red to lavender, the inner paler; styles 17–25 mm, long-exserted, extending beyond stamens, with stigmas not receptive before 3–6 d after anthesis; capsules 1.5–3 cm. **Flowering** April–May. **California**. Two

disjunct areas: A) Interior Coast Ranges, San Benito, Fresno, and Stanislaus counties; and B) Sierra Foothills, Kern County.

Representative collections: CALIFORNIA. **Fresno Co.**: Tumey Hills, *Sanders 35150* (CAS, DAV, RSA, UC, UCR); Mercy Springs, *Smith-Huerta s.n.* (RSA); S. of Panoche Rd., *Lewis & Lewis 911* (UC); Ciervo Hills, *Crosby & Morin 14358* (RSA). **Kern Co.**: Caliente Hills, *Vasek 670416-2* (UCR); Bakersfield, *Davy 1711* (UC); Long Tom Mine, *Smith 351* (JEPS, RSA). **San Benito Co.**: Griswold Hills, *Sanders 35187* (DAV, UCR); *Constance & Morrison 2267* (POM, UC); *Raven 10866* (RSA, UC); *McCaskill 440* (DAV); *Holtsford 860506-6* (UCR). **Stanislaus Co.**: Arroyo del Puerto, *Sharsmith 1753* (UC).

Clarkia tembloriensis* subsp. *tembloriensis Vasek (Fig. 2).

Flowers smaller than those of *Clarkia tembloriensis* subsp. *longistyla*, with the hypanthia 2–3 mm; sepals 10–14 mm, petals 8–16 mm long, 5–8 mm wide; or, sometimes narrower, or reduced and unexpanded, the claw scarcely distinguishable from the blade, which may be only 1–3 mm wide; style short, usually less than 16 mm, not exceeding the stamens, or only slightly so, the stigma receptive usually the first or second day the flower opens. $2n = 18$ (Vasek 1964a). **Flowering** April–May. **California**. Interior Coast Ranges, western Kern County to Alameda and San Joaquin Counties. 400 to 3300 ft in elevation.

Representative collections: CALIFORNIA. **Alameda Co.**: Corral Hollow, *Eastwood & Howell 5291* (RSA). **Fresno Co.**: Tumey Hills, *Vasek 620505-3* (UCR); Ciervo Hills, *Preston 2070* (DAV); Cantua Creek, *Holtsford s.n.* (UCR); *Vasek 620505-2* (UCR); W. of Coalinga, *Vasek 620505-5* (UCR); Warthan Creek, *Helmkamp s.n.* (UCR); Coyote Canyon, *Janeway 1529* (CHSC). **Kern Co.**: Carneros Rocks, *Vasek 580503-2* (UCR); Carneros Canyon, *Holtsford s.n.*

(UCR). **Kings Co.:** Kettleman Hills, *Hoover 3301* (UC); *Sanders 22727* (UCR). **Merced Co.:** Los Banos Creek, *Janeway 1597* (CHSC). **San Benito Co.:** Griswold Hills, *Hesse 2451* (UC). **San Joaquin Co.:** Corral Hollow, *Hoover 3358* (UC), *Taylor 8790* (JEPS, UC). **San Luis Obispo Co.:** Red Canyon (Cholame), *Holtsford s.n.* (UCR); Syncline Hill, *Preston 1122* (DAV, UCR); Hughes Canyon, *Holtsford s.n.* (UCR); Temblor Range (McKittrick Rd.), *Holtsford s.n.* (UCR); *Smith-Huerta s.n.* (RSA); Temblor Range (3,000 ft), *Johannsen 1141* (UC); W. Soda Lake, *Vasek 620502-1* (UCR).

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